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## Feeding Ecology of Stream-Dwelling Pacific Giant Salamander Larvae (*Dicamptodon tenebrosus*)

MICHAEL S. PARKER

Pacific giant salamander larvae in a northern California stream were found to consume a wide variety and size range of prey in a one-year diet study. Aquatic insects made the greatest contribution to salamander diets, both numerically and by volume, with ephemeroptera nymphs being the most frequently consumed prey type. Although terrestrial invertebrates that fell into the stream constituted a small proportion of the diet numerically, they comprised a large proportion of diet volume throughout the year. Stomach contents mass and the proportion of intact prey in the stomach contents did not vary with time of day. In contrast, larval salamanders exhibited a strong diel activity pattern, being inactive and under cover during the day and active on the streambed surface at night. As larval salamanders grew, they included larger prey in their diet but continued to consume large numbers of very small prey. Small salamanders were able to consume a large proportion of the size range of most common prey, whereas only large salamanders were capable of consuming rare, large prey (e.g., large odonates, megalopterans, fish, and small salamanders). There was considerable dietary overlap among three co-occurring salamander size classes suggesting that food resources were not strongly partitioned among them. Relative abundances of prey in the diet were not correlated with their relative abundances in the environment, indicating that larval salamanders feed preferentially on certain prey taxa while avoiding, not encountering, or being unable to capture others. Electivity values were consistently positive for ephemeropterans and large, mobile invertebrate predators but were consistently negative for small, cryptic invertebrates and case-building caddisflies. In addition, mean sizes of three common mayflies were consistently larger in salamander stomach contents than in the benthos, indicating that predation on benthic invertebrates by larval *Dicamptodon tenebrosus* is size selective.

THE Pacific giant salamander, *Dicamptodon tenebrosus* [formerly *D. ensatus*; see Good (1989)], is a prominent member of amphibian assemblages in forested regions of the Pacific Northwest of North America. Its range extends from southwest British Columbia, through the Cascade and coastal mountain ranges, to northwest California (Nussbaum et al., 1983; Good, 1989). Unlike most species of the closely related Ambystomatidae (see Larson, 1991; Shaffer et al., 1991) that breed in ponds, *D. tenebrosus* breeds primarily in streams (Nussbaum, 1976). Larval *D. tenebrosus* are often the dominant vertebrate predator in high gradient streams throughout their range. For example, Murphy and Hall (1981) reported that larval *D. tenebrosus* represented greater than 90% of total predator biomass in a number of small streams in western Oregon and northern California. Likewise, Corn and Bury (1989) showed that *D. tenebrosus* larvae dominated vertebrate assemblages in western Oregon streams and reported average numerical densities of 2.3 animals/m<sup>2</sup> and biomass densities of 8.2 g/m<sup>2</sup>. Although a

small number of studies have described stomach contents of stream- (Metter, 1963; Franz, 1970; Antonelli et al., 1972) and pond-dwelling larval *Dicamptodon* (Johnson and Shreck, 1969), they provide little more than lists of prey eaten and fail to reveal details of the feeding ecology of this potentially important top predator.

In general, much of what is currently known about the feeding ecology of aquatic salamander larvae is based on detailed studies of relatively few genera; most notably *Ambystoma* (e.g., Dodson and Dodson, 1971; Leff and Bachmann, 1988; McWilliams and Bachmann, 1989a), *Notophthalmus* (e.g., Hamilton, 1940; Burton, 1977; Attar and Maly, 1980), and *Triturus* (e.g., Avery, 1968; Ranta and Nuutinen, 1985; Kuzmin, 1991). These are primarily pond-dwelling taxa that feed mainly on zooplankton or switch between planktivory and benthic feeding either on a diel basis or over longer time scales as they mature. In contrast to pond-dwelling taxa, stream-dwelling salamander larvae feed exclusively on benthic organisms throughout the larval period. Consequently, they are likely

to have fundamentally different feeding habits and exert stronger predation pressure on benthic prey assemblages.

In this study, I conducted a detailed analysis of the feeding ecology of larval *D. tenebrosus* in a small, headwater stream where they are the dominant predator. Specifically, I examined (1) diet composition and seasonal changes in diet; (2) daily patterns of activity and feeding intensity; (3) predator-prey size relationships, ontogenetic diet shifts, and partitioning of the food resource among larval size classes; and (4) selective predation with respect to both prey type and prey size.

#### METHODS

*Study site and natural history.*—This study was conducted in Fox Creek, a small, high gradient tributary of the South Fork Eel River. The entire 280-ha watershed of Fox Creek is within the boundaries of the Northern California Coast Range Preserve located in northern Mendocino County, California (38° 45' N, 123° 40' W). Fox Creek drains a watershed of old-growth Douglas fir and mixed evergreen forest, and the stream channel is heavily shaded by a dense forest canopy and steep canyon walls. The flow regime reflects the Mediterranean climate of coastal California, where the dry season extends from April through Oct. During this period Fox Creek has a discharge of approximately 5–7 liters/sec. Periodic winter storms from Oct. through March produce higher, fluctuating flows that often exceed base flow several-fold. During low flow, the channel is a series of pools connected by relatively steep plunges or short riffles. The substratum is a heterogeneous mixture of large cobbles and boulders overlying finer gravel and sandy sediments.

Larval *D. tenebrosus* are present in Fox Creek throughout the year. Between 1987 and 1990, larval salamander densities ranged from 0.9–1.24/m<sup>2</sup> (unpubl. data). Young-of-the-year (YOY), larvae that are approximately 45–50 mm total length (TL), begin to appear in lower reaches of the stream in April and May. Second-year larvae, typically 80–120 mm TL, are present year-round. Some second- and third-year larvae, ranging in size from 105–153 mm TL, metamorphose in late summer (July through Sept.), whereas others become paedomorphic. Individuals exceeding 200 mm TL are fairly common. Larval *D. tenebrosus* dominate the vertebrate assemblage in Fox Creek, both numerically and in biomass. Resident and anadromous rainbow trout (*Oncorhynchus mykiss*) also occur but at much lower densities than salamanders.

The benthic invertebrate assemblage in Fox Creek is comprised of eight insect orders and several noninsect taxa which provide a broad range of prey types and sizes available to vertebrate predators.

*Diet composition.*—I collected salamanders for diet analysis on 11 dates from Nov. 1988 through Sept. 1989. Collections were made at least three different times during the day (within an hour after sunrise, at midday, and within an hour after sunset). Salamanders were collected by searching 15–20 m stream segments, systematically overturning potential cover objects and probing crevices with a blunt stick, and capturing exposed salamanders with a small dipnet. Within an hour of capture, the animals were anesthetized in a dilute solution of MS-222 (methane tricaine sulfonate), and their stomach contents were extracted by flushing with filtered stream water (Legler and Sullivan, 1979). Stomach contents were retained on 50- $\mu$ m mesh nylon screening and kept frozen prior to analysis. After stomach contents were removed, each animal was weighed (to the nearest 0.1 g) and measured [TL and snout-vent length (SVL) to the nearest 0.5 mm].

In the laboratory, prey were identified to the lowest practical taxonomic level (family or genus for aquatic and order for terrestrial organisms). Volumes of intact prey were estimated by assuming they were either rectangular or cylindrical solids, depending on body shape (Maiorana, 1978; Petranka, 1984), and measuring their length (excluding antennae and cerci), average width, and average thickness using a calibrated ocular micrometer fitted to a dissecting microscope. For partially digested insect prey, volumes were estimated by measuring head widths and using predetermined volume vs head width regressions (Parker 1992). Total stomach contents mass was measured by collecting all prey and prey parts on preweighed filters, drying them to constant weight (65 C for 48 h) and weighing them to the nearest 0.01 mg.

*Diel activity and feeding patterns.*—To examine daily patterns of feeding activity, I compared relative stomach contents mass (mg dry mass of stomach contents/g salamander live mass  $\times$  100) and the proportion of intact prey in stomachs of salamanders collected at 4-h intervals over a 24-h period on four dates (3–4 May, 11–12 July, 3–4 Aug., and 19–20 Sept. 1989). On four other dates (25 May, 18 June, 20 July, and 24 Aug.), I conducted visual surveys to assess daily movements of larval salamanders to and from cover and to determine whether shifts in activity cor-

responded to differences in feeding intensity. At four times over a 24-h period, different 25-m stream segments were surveyed by slowly walking along the bank in an upstream direction thoroughly scanning the streambed for exposed salamanders. Times were dawn (0530–0700 h), midday (1130–1300 h), dusk (1945–2130 h), and midnight (2230–2400 h). At night and in the early morning and evening when ambient light levels were low, a headlamp was used to locate salamanders. Following the initial count, all exposed salamanders were captured, and the stream segment was thoroughly searched by turning all potential cover objects and collecting animals that were under cover. Each salamander was measured and weighed to compare size distributions of animals active on the streambed with those under cover during each time period.

*Prey preference.*—On six dates during low flow (4 May, 2 June, 28 June, 11 July, 5 Aug., and 20 Sept.), and within 24 h of collecting salamanders for diet analysis, I collected six benthic invertebrate samples to compare prey availability with salamander diet composition (except 2 June when  $n = 4$  benthic samples). To collect benthic prey in proportions similar to their availability to larval salamanders, I collected samples from microhabitats similar to those from which salamanders had been collected. Each sample consisted of a  $25 \times 25$  cm area of streambed containing at least one large stone of the size most often used as cover by larval salamanders [mean diameter  $1 \pm \text{SD} = 18.15 \pm 6.23$  cm (Parker, 1991)]. A square template was used to delineate the sample area, and all large stones within the template were rolled into a dipnet (0.3 mm mesh). The remaining substratum was thoroughly overturned washing loosened debris and organisms also into the net. Net contents were preserved (80% ethanol) and returned to the laboratory where macroinvertebrates were removed and identified to the lowest possible taxonomic level.

To determine the relationship between prey availability and diet composition, I calculated Spearman's coefficient of rank correlation (Conover, 1982) between the relative abundances of prey taxa in the benthos and their relative abundances in salamander stomach contents. A significant positive correlation would indicate that salamanders encounter and consume prey in direct proportion to their relative abundance in the environment (Elliott, 1970; Allan, 1981). The lack of a significant correlation would suggest that salamanders preferentially consume some prey while others are

either avoided, encountered at low frequency, or are able to escape being captured and ingested.

To determine whether certain prey types were either consistently over- or underrepresented in the diet in proportion to their relative abundance in the environment, I calculated Vanderploeg and Scavia's (1979) relativized electivity index ( $E^*$ ).  $E^*$  is calculated as

$$E^* = [W_i - (1/n)]/[W_i + (1/n)]$$

$$\text{with } W_i = r_i/p_i/\sum r_i p_i \quad (1)$$

where  $r_i$  is the relative abundance of prey type  $i$  in the diet,  $p_i$  is the relative abundance of prey type  $i$  in the environment, and  $n_i$  is the number of prey types included in the analysis. This index is considered the best among several alternatives for field data, particularly when numbers and relative abundances of prey types vary among sampling periods (Lechowicz, 1982; Confer and Moore, 1987). Index values range from  $-1.0$  to  $+1.0$ , with values near zero (i.e.,  $-0.05$  to  $+0.05$ ) indicating neutral selection. Because  $E^*$  is vulnerable to sampling errors for prey that are rare in the diet or in the environment (Lechowicz, 1982), only taxa that had a relative abundance of at least 1% in both the stomach contents and benthos were included in the analysis. This cutoff was selected because taxa with relative abundances greater than 1% were generally present in all six benthic samples on a given date, whereas taxa with lower relative abundances were rarely present in all replicate samples.

*Ontogenetic diet shifts.*—During the summer, three fairly distinct size classes of larval *D. tenebrosus* are present in Fox Creek. YOY larvae range in size from approximately 25–45 mm SVL (45–80 mm TL), second-year larvae range from approximately 46–70 mm SVL (80–120 mm TL), and larvae older than two years are generally greater than 70 mm SVL ( $>125$  mm TL; Parker, 1992). To determine whether salamander diets change ontogenetically, I compared diet composition of these three size groups from collections made on 11–12 July, 4–5 Aug., and 19–20 Sept. I used a simple similarity index (Schoener, 1968):

$$C_{xy} = 1 - 0.5 \sum |p_{ix} - p_{iy}| \quad (2)$$

based on proportions of prey categories ( $i$ ) in diets of the different salamander size classes ( $x$  and  $y$ ), to quantify dietary overlap between them. In addition, I examined predator-prey size relationships by regressing volumes of the largest

TABLE 1. PREY COLLECTED FROM LARVAL *Dicamptodon tenebrosus* STOMACHS. Proportions of total prey based on sum of all sampling dates ( $n = 11$ ) and values in parentheses are minimum–maximum values among sampling dates.

Prey taxon	Proportion of sample dates prey occurred in diet	Proportion of total prey
Ephemeroptera	100.0	59.1 (19.4–88.6)
<i>Paraleptophlebia</i>	100.0	24.2 (12.5–56.5)
<i>Baetis</i>	100.0	15.1 (6.3–18.1)
<i>Anaetetus</i>	88.2	6.5 (0.0–20.7)
Heptageniidae	100.0	10.8 (1.4–24.3)
Ephemerellidae	63.6	2.4 (0.0–3.1)
Trichoptera	100.0	11.7 (0.6–42.8)
<i>Polycentropus</i>	90.9	3.6 (0.0–8.1)
<i>Rhyacophila</i>	100.0	1.6 (0.6–3.3)
<i>Lepidostoma</i>	81.8	1.2 (0.0–5.2)
<i>Neophylax</i>	72.7	1.6 (0.0–23.5)
Other Limnephilidae	54.5	<1.0 (0.0–0.8)
<i>Heteroplectron</i>	81.8	<1.0 (0.0–5.4)
<i>Glossosoma</i>	72.7	<1.0 (0.0–4.4)
Others	63.6	<1.0 (0.0–3.1)
Plecoptera	100.0	4.5 (0.8–11.9)
<i>Calineuria</i>	100.0	2.1 (0.8–8.1)
<i>Malenka</i>	81.8	<1.0 (0.0–2.3)
Chloroperlidae	81.8	<1.0 (0.0–1.8)
<i>Parleuctra</i>	54.5	<1.0 (0.0–3.8)
Others	0.9	<1.0 (0.0–0.2)
Diptera	100.0	8.1 (2.8–25.6)
Chironomidae	100.0	6.5 (2.8–24.2)
<i>Simulium</i>	54.5	<1.0 (0.0–0.9)
Dixidae	45.5	<1.0 (0.0–0.4)
Tipulidae	27.3	<1.0 (0.0–0.8)
Others	18.2	<1.0 (0.0–1.0)
Coleoptera	72.7	3.6 (0.0–6.2)
<i>Eubrianax</i>	72.7	2.8 (0.0–4.9)
Elmidae	36.4	<1.0 (0.0–1.0)
Others	63.6	<1.0 (0.0–1.9)
Odonata	88.2	1.0 (0.0–2.2)
<i>Octogomphus</i>	72.7	<1.0 (0.0–1.4)
<i>Cordulegaster</i>	45.5	<1.0 (0.0–0.6)
Hemiptera	27.3	<1.0 (0.0–1.0)
<i>Gerris</i>	18.2	<1.0 (0.0–0.9)
<i>Microvelia</i>	0.9	<1.0 (0.0–0.1)
Megaloptera		
<i>Orohermes</i>	36.4	<1.0 (0.0–1.1)
Non-Insecta	100.0	3.4 (0.0–9.4)
Ostracoda	90.9	2.6 (0.0–8.9)
Acarina	54.5	<1.0 (0.0–1.1)
Nematomorpha	36.4	<1.0 (0.0–0.3)
Turbellaria	0.9	<1.0 (0.0–0.4)
Vertebrates		
Oncorhynchus	27.3	<1.0 (0.0–1.2)
Dicamptodon	27.3	<1.0 (0.0–0.3)
Terrestrial organisms*	100.0	8.8 (1.9–19.0)

\* Includes Coleoptera, Lepidoptera, Orthoptera, Hymenoptera, Homoptera, Dermaptera, Collembola, Ephemeroptera and Trichoptera adults, Diplopoda, Gastropoda, Oligochaeta, Isopoda, and Arachnida.

and smallest prey items eaten vs salamander size (SVL). Only salamanders that had at least three identifiable prey items in their stomachs were included in the analysis. Regression equations were similar on all three dates, so data were pooled for this analysis. I also examined taxon-specific predator-prey size relationships by regressing volumes of the most common species within the four most abundant insect orders (Ephemeroptera, Diptera, Plecoptera, and Trichoptera) vs salamander size.

*Size-selective predation.*—To examine size-selective predation by larval salamanders, I compared size distributions of three common mayfly prey (*Paraleptophlebia* sp., *Baetis* spp., and Heptageniidae) in the stomach contents with their size distributions in the benthos. This analysis was restricted to this small group of prey because they were consistently the most frequent prey consumed by larval salamanders (see Results) and had consistently high densities in the benthos. In addition, gut clearance rates did not differ among size classes of these prey types (Parker, 1992, 1993). Moreover, comparing predator preference for different size individuals of the same prey type minimizes effects on selection resulting from factors other than size that vary among prey taxa (i.e., body shape, mobility, coloration, chemical cues, predator avoidance behavior, and differences in microhabitat use). One-tailed Mann-Whitney U tests were employed to test the hypothesis that mean prey size is larger in stomach content samples than in the benthos.

## RESULTS

*Diet composition.*—I examined the stomach contents of 502 larval salamanders during this study and identified 3652 individual prey items (Table 1). Abundances and volumes of major prey categories varied considerably among sample dates (Table 2). Aquatic insects were consistently the largest component of the diet, both numerically and by volume. Mayfly nymphs (Ephemeroptera) were the most frequently consumed prey, making up 30–69% of total prey consumed on any date. However, mayflies comprised only 1–26% of diet volume (Table 2). Caddisfly larvae (Trichoptera), stonefly nymphs (Plecoptera), and dipteran larvae were the next most frequently consumed prey types. Trichopterans and plecopterans often comprised a large proportion of diet volume, whereas dipterans were never more than a very small proportion of diet volume. Large prey items such as dragonfly nymphs (Odonata) and Megaloptera lar-



vae were infrequently included in the diet but occasionally comprised a considerable proportion of total prey volume. For example, in Feb., a single large megalopteran (*Orohermes crepusculus*) comprised 37% of total prey volume, and, in May and Sept., *Octogomphus specularis* (Odonata: Gomphidae) individuals made up less than 2% of total prey numbers but were greater than 20% of total prey volume.

A wide variety of terrestrial organisms fell into the stream and were eaten, including Diplopoda, Gastropoda, Annelida, Arachnida, Hymenoptera, Coleoptera, Lepidoptera, and adult Trichoptera and Ephemeroptera. Terrestrial organisms were consumed at low frequency throughout the year but comprised a consistently large proportion of diet volume (6–58%). On two sampling dates, 14–15 Dec. and 28–29 June, terrestrial organisms approached or exceeded 50% of total diet volume. On both occasions, there had been moderate-to-heavy rainfall just prior to or during the time I collected samples. A large proportion of the salamanders collected had consumed terrestrial earthworms (*Lumbricus* sp.) that had been washed into the stream and dominated total diet volume.

Cannibalism was observed on four occasions between March and July. In each case, a large individual (>100 mm TL) consumed a single YOY larva (<65 mm TL). Juvenile rainbow trout (*Oncorhynchus mykiss*) were also found in the stomachs of larger larvae (>100 mm TL) on three occasions, and a trout egg was found in a salamanders stomach on 30 March.

**Diel activity and feeding patterns.**—On all four diel surveys, a large proportion of the population was out of cover at night whereas the majority of salamanders was under cover during the other time periods (Fig. 1). There were no size differences between salamanders in or out of cover at night (t-tests,  $P > 0.10$  on all dates), indicating that activity patterns were not size or age specific.

In contrast to the distinct diel activity pattern, there was no consistent diel pattern in feeding intensity. Larval salamanders had food in their stomachs throughout the day, and there were no significant differences in relative stomach contents mass among sampling times on any of the four dates (Fig. 2). Relative gut content mass was considerably higher in early May, however, suggesting there may be seasonal patterns in feeding intensity, perhaps associated with differences in prey availability. Benthic invertebrate density was also greatest on the May sampling date (Table 3). Of the 312 salamanders

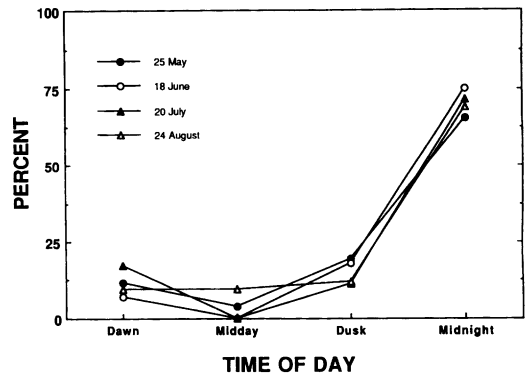


Fig. 1. Proportions of larval *Dicamptodon tenebrosus* visible on the streambed at different times of day illustrating diel movement into and out of cover. Points are percent of total salamanders observed on each date.

examined on these four dates, only two individuals had empty stomachs. Both were in the process of transforming from aquatic larvae into terrestrial adults and were probably not actively feeding. These animals were not included in this analysis. On two of four dates, differences in proportions of intact prey in salamander stomachs were significant (11–12 July,  $F = 3.14$ ,  $P_{5,78} = 0.015$ ; 3–4 Aug.,  $F = 3.52$ ,  $P_{5,80} = 0.006$ ), but there was no consistent pattern of when the greatest proportion of intact prey was present. Midday and dusk samples during July had significantly fewer intact prey than samples collected at midnight, dawn, midmorning, or afternoon, whereas, in Aug. the midnight sample had a significantly higher proportion of intact prey than any of the other times (Fig. 2; Fisher's least significant difference test;  $P < 0.05$  on both dates).

**Prey preferences.**—Densities of common benthic macroinvertebrates fluctuated a great deal between May and Sept. (Table 3). The most abundant organisms throughout this period were chironomids, mayflies, water penny beetle larvae (*Eubrianax edwardsi*), nemourid stonefly nymphs (*Malenka* spp), *Lepidostoma* (Trichoptera), and small, cryptic taxa including water mites, ostracods, and oligochaetes. There was no correlation between relative abundances of prey types in the environment and their relative abundances in the salamander diet (Spearman's rank correlation,  $P > 0.05$  on all six dates). Electivities for the four most abundant mayfly genera were typically positive as were electivities for *Polycentropus* sp. (Trichoptera: Polycentropidae) and *Calineuria californica* (Plecoptera: Perlidae), two of the most abundant inverte-

TABLE 2. PROPORTIONS OF MAJOR PREY GROUPS IN STOMACH CONTENTS OF LARVAL *Dicamptodon tenebrosus* ON 11 DATES FROM NOV. 1988 TO SEPT. 1989. %N is the proportion of total identifiable prey and %V is the proportion of total prey volume.

Taxon	12-13 Nov.		14-15 Dec.		15-16 Feb.		29-30 March	
	%N	%V	%N	%V	%N	%V	%N	%V
Ephemeroptera	29.9	11.6	48.7	1.1	63.9	25.7	41.1	7.0
Plecoptera	9.3	10.8	8.1	22.8	3.7	12.9	7.4	6.3
Trichoptera	12.1	35.7	18.9	17.7	20.6	16.9	16.8	27.3
Diptera	25.5	4.9	10.8	<0.1	8.1	1.4	11.6	4.7
Coleoptera	4.8	2.7	—	—	—	—	—	—
Odonata	—	—	—	—	—	—	1.1	6.7
Megaloptera	—	—	—	—	0.7	36.7	1.1	11.2
Hemiptera	—	—	—	—	—	—	—	—
Ostracoda	8.9	0.1	2.7	<0.1	0.7	<0.1	1.1	<0.1
Acarina	0.6	<0.1	—	—	—	—	—	—
Dicamptodon	—	—	—	—	—	—	—	—
Oncorhynchus	—	—	—	—	—	—	1.1	1.5
Terrestrial Organisms	8.9	34.3	10.8	58.1	2.2	6.4	19.0	35.9
No. of salamanders	25		11		22		14	

brate predators in Fox Creek (Fig. 3). Common prey that had consistently high negative electivity values included case-building trichopterans (*Limnephilidae* and *Lepidostoma*), Chironomidae, *Eubrianax*, *Malenka*, and water mites (Fig. 3).

*Predator-prey size relationships and ontogenetic diet shifts.*—As larval *D. tenebrosus* increase in size, they incorporate larger prey into their diet but continue to consume large numbers of small prey. There were weak, but significant, positive correlations between salamander length and volumes of the largest and smallest prey ingested (Fig. 4). Regressions of prey volume vs salamander size for the most numerically abundant taxa within the four major insect orders produced mixed results. There were significant positive correlations between salamander size and *Paraleptophlebia* and Chironomidae volumes but not between salamander size and *Calineuria* or *Polycentropus* volumes (Fig. 5).

Comparisons of diet composition among co-existing larval size classes revealed that they all consumed the same prey types but that relative proportions of certain prey differed slightly among them (Table 4). Ephemeropterans, particularly *Paraleptophlebia*, were the most frequently consumed prey by all three size classes present during the summer. Small larvae consumed proportionately more small prey, such as chironomids and ostracods, whereas medium and large larvae consumed larger proportions of case-building trichopterans (*Limnephilidae* and *Lepidostoma*) and large predatory invertebrates (*Calineuria* and *Polycentropus*). Dietary overlap among the three size classes was high

(size class I vs size class II = 0.798, size class II vs size class III = 0.862, and size class I vs size class III = 0.675), suggesting that the food resource is not strongly partitioned among them and that major changes in the diet do not accompany changes in body size.

*Size-selective predation.*—All three mayfly taxa examined were consistently larger in salamander stomach contents than in the benthos ( $P < 0.001$  on all dates, Mann-Whitney U test). This result combined with the above observation that large, mobile taxa are consistently overrepresented in the diet demonstrates the size-selective nature of salamander predation on these prey (see also Parker, 1993).

## DISCUSSION

Like most salamander larvae, larval *D. tenebrosus* are generalist predators that consume a wide variety and size range of invertebrate prey. Although their diet was dominated numerically by aquatic organisms, terrestrial organisms consistently contributed a large proportion to the total volume of prey consumed. Antonelli et al. (1972) also reported that terrestrial organisms were important to the diet of larval *Dicamptodon*, as well as to sculpin and trout in a small Washington stream. These observations illustrate the importance of allochthonous inputs to headwater stream food webs, both as the food source for many primary consumers (Cummins, 1974) and, as shown here, an important food source for top carnivores.

Based on a small number of descriptive studies, Metter (1963) and Antonelli et al. (1972)

TABLE 2. CONTINUED.

17-19 April		4-5 May		1-2 June		28-29 June		11-12 July		3-4 Aug.		19-20 Sept.	
%N	%V	%N	%V	%N	%V	%N	%V	%N	%V	%N	%V	%N	%V
50.0	9.0	53.3	9.3	63.6	13.3	55.5	10.2	61.6	17.6	62.0	23.5	69.1	23.2
6.3	19.5	5.2	6.7	4.5	10.2	1.6	2.6	3.0	5.4	5.0	6.3	4.0	1.6
19.8	11.2	17.1	13.4	10.9	22.7	9.7	17.3	8.9	19.7	10.0	29.7	5.8	5.6
6.8	5.2	6.2	0.5	7.6	2.6	4.1	0.9	5.3	0.2	8.3	0.8	9.8	0.4
2.7	1.1	5.2	5.6	3.4	2.4	2.5	2.5	2.7	2.7	4.0	3.7	5.6	8.0
1.4	12.4	1.4	21.4	1.5	3.7	0.3	2.4	0.8	9.3	0.5	5.8	1.2	24.5
—	—	0.4	4.5	—	—	—	—	0.5	7.4	—	—	—	—
0.9	4.5	0.2	<0.1	<0.1	<0.1	—	—	3.0	2.0	—	—	—	—
1.4	<0.1	0.6	<0.1	<0.1	<0.1	—	—	3.2	<0.1	6.0	<0.1	2.1	<0.1
0.5	<0.1	1.2	<0.1	1.2	<0.1	1.3	<0.1	1.8	<0.1	1.1	<0.1	1.3	<0.1
—	—	0.2	8.4	<0.1	10.6	0.3	15.2	—	—	—	—	—	—
—	—	—	—	<0.1	4.2	—	—	—	—	—	—	0.2	14.3
10.3	35.9	8.9	31.0	6.7	30.2	25.6	48.8	10.2	35.4	3.6	29.8	1.9	22.1
25		68		47		42		87		87		74	

concluded that diet composition of larval *Dicamptodon* reflects the relative abundances of different prey types in the environment. Antonelli et al. (1972) is the only previous study to attempt to compare diet composition with prey availability, however; and their data do not

support this conclusion. In their study, numerous macroinvertebrate taxa collected in benthic samples were not found in salamander stomachs, and many taxa had much higher relative abundances in salamander stomach contents than in the benthos. My results also contradict the conclusion that Pacific giant salamander larvae consume prey in similar proportions to their relative abundances in the environment. Instead, certain prey were consistently overrepresented while others were consistently underrepresented in the diet. These results are in general agreement with a large number of studies that have shown stream-dwelling predators,

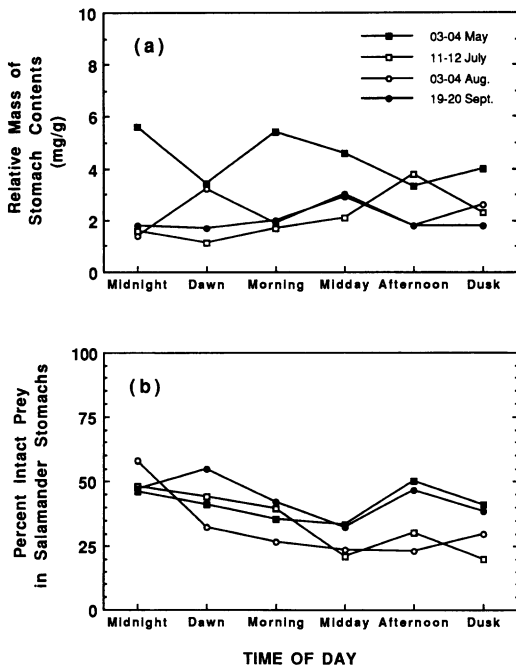


Fig. 2. Diel feeding activity of *Dicamptodon tenebrosus* presented as (a) relative stomach contents mass (mg stomach content dry mass/g salamander live mass  $\times$  100), and (b) proportion of intact prey in salamander stomachs. For clarity, error bars are not shown.

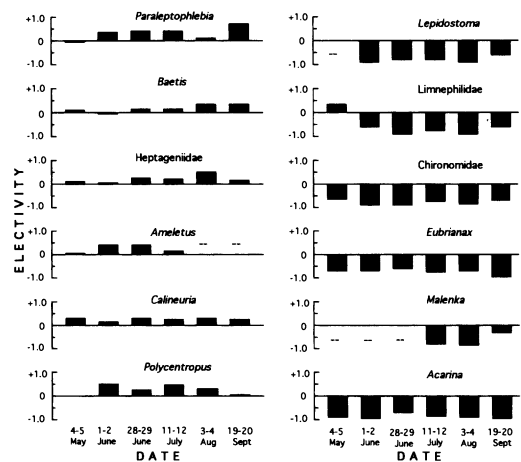


Fig. 3. Electivities (Vanderploeg and Scavia's E\*) for common prey consumed by larval *Dicamptodon tenebrosus* (dashed lines indicate dates on which a prey was less than 1% of diet or benthos).



TABLE 3. DENSITIES (no./m<sup>2</sup>) OF COMMON BENTHIC MACROINVERTEBRATES IN FOX CREEK DURING SPRING-SUMMER 1989. Values are means (rounded to nearest whole number) with 1 SE in parentheses.

Taxon	4 May	2 June	28 June	11 July	4 Aug.	20 Sept.
<b>Ephemeroptera</b>						
<i>Paraleptophlebia</i>			468 (161.4)	355 (52.7)	336 (93.0)	310 (89.2)
<i>Baetis</i>	984 (132.1)	527 (183.7)	632 (303.9)	349 (110.2)	160 (47.6)	211 (41.6)
<b>Heptageniidae</b>	317 (86.6)	163 (40.9)	64 (21.9)	272 (52.5)	141 (20.8)	80 (32.8)
<i>Anelotus</i>	319 (80.1)	202 (36.9)	248 (13.3)	54 (11.9)	16 (7.2)	0 (0)
<b>Ephemereilidae</b>	34 (21.0)	30 (13.2)	24 (8.0)	157 (81.9)	157 (70.4)	10 (5.2)
<b>Plecoptera</b>						
<i>Calineuria</i>	77 (15.7)	38 (8.1)	57 (8.0)	62 (7.5)	57 (9.9)	73 (9.9)
<i>Malenka</i>	35 (9.6)	210 (43.1)	244 (72.1)	221 (58.1)	205 (63.7)	109 (28.4)
<i>Paraleucira</i>	117 (59.1)	41 (9.3)	16 (9.2)	58 (18.8)	27 (12.2)	80 (29.6)
<b>Chloroperliidae</b>	101 (26.6)	4 (1.5)	0 (0)	3 (2.9)	8 (5.7)	35 (14.2)
<b>Trichoptera</b>						
<i>Polycentropus</i>	104 (29.4)	76 (10.6)	60 (19.9)	67 (16.9)	57 (12.7)	77 (23.5)
<i>Rhyacophila</i>	19 (4.9)	65 (8.3)	108 (46.1)	96 (14.6)	75 (19.1)	77 (32.9)
<i>Lepidostoma</i>	354 (109.3)	419 (151.4)	704 (207.5)	1366 (436.1)	363 (146.7)	224 (55.7)
<i>Neophylax</i>	32 (13.1)	41 (14.8)	108 (69.9)	93 (29.7)	59 (19.7)	38 (24.1)
<b>Other Limnephilidae</b>	43 (30.8)	10 (5.0)	16 (6.5)	3 (3.2)	35 (19.1)	134 (166.7)
<i>Parithina</i>	117 (50.8)	53 (7.7)	44 (12.0)	32 (10.9)	43 (30.5)	19 (7.2)
<i>Heteroplectron</i>	69 (25.7)	74 (28.2)	40 (24.0)	115 (41.9)	160 (121.9)	140.8 (63.5)
<i>Glossosoma</i>	0 (0)	15 (4.9)	28 (18.9)	112 (40.0)	16 (10.9)	22 (18.7)
<b>Coleoptera</b>						
<i>Eubrianax edwardsi</i>	944 (193.7)	412 (82.1)	388 (191.3)	310 (65.4)	301 (52.6)	458 (87.4)
<b>Elmidae larvae</b>	504 (226.2)	108 (34.4)	76 (60.4)	67 (14.9)	51 (15.7)	125 (49.4)
<b>Diptera</b>						
<b>Chironomidae</b>	1117 (236.4)	1377 (244.2)	1216 (215.6)	1696 (145.9)	1896 (277.3)	2150 (581.5)
<b>Non-Insects</b>						
<b>Acarina</b>	688 (131.7)	201 (52.2)	328 (93.5)	154 (17.0)	163 (35.3)	176 (24.3)
<b>Ostracoda</b>	176 (46.6)	97 (21.7)	52 (16.5)	48 (18.2)	56 (21.4)	192 (53.8)
<b>Oligochaeta</b>	53 (34.5)	81 (18.6)	192 (42.8)	90 (62.3)	114 (38.6)	176 (65.0)
<b>Total macroinvertebrates</b>	7221 (604.0)	5089 (459.3)	5540 (736.9)	6097 (400.7)	4853 (566.7)	6390 (1089.9)

both vertebrate (e.g., Ware, 1972; Gilson and Benson, 1979; Newman and Waters, 1984) and invertebrate (e.g., Siegfried and Knight, 1975; Molles and Pietruszka, 1983; Allan et al., 1987), to have identifiable preferences with respect to both prey type and size.

Factors that influence prey preference include the rate at which a particular prey type is encountered, the likelihood the prey will be attacked once encountered, and the ability of the predator to capture and consume the prey once it has been attacked. Although analyses of stomach contents alone cannot reveal which of these factors is most important in determining prey preference, knowledge of the natural histories and habits of both predator and the array of available prey can provide valuable insights, particularly with respect to the relative likelihood of a particular prey being encountered. Microhabitat overlap and conspicuousness strongly influence prey encounter rates (Sih and Moore, 1990). Larval *D. tenebrosus* are sit-and-wait predators (Huey and Pianka, 1981) that remain relatively inactive and under cover throughout much of the day. Theory predicts that sit-and-wait predators should encounter active prey at a higher rate than inactive prey, whereas the opposite is true for mobile, actively searching predators (e.g., Gerritsen and Strickler, 1977). Mobile prey that move around on substrate surfaces would be more likely to enter a larval salamander's perceptive field than sedentary or cryptic prey and should, thus, be more susceptible to salamander predation. This appears to be the case in Fox Creek. Ephemero-

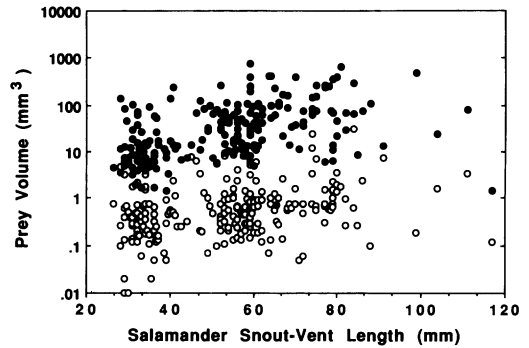


Fig. 4. Relationship between larval salamander length and minimum (open circles) and maximum (dark circles) volumes of prey in their stomach contents  $R^2_{\max} = 0.199$ ,  $P = 0.021$ ;  $R^2_{\min} = 0.088$ ,  $P = 0.048$ .

pterans were the most frequently consumed prey and had consistently positive electivities throughout this study. Ephemeropterans are among the most mobile benthic macroinvertebrates in Fox Creek and in streams in general (Hynes, 1970). In addition, two of the most abundant invertebrate predators in Fox Creek, *Calineuria* and *Polycentropus*, which are also relatively mobile or conspicuous on stone surfaces, had consistently positive or neutral electivities.

In contrast, prey consistently underrepresented in the diet tended to be small, relatively inactive taxa that inhabit either interstitial spaces among small substrate particles (i.e., many Chironomidae, Acarina and Oligochaeta), accumulations of detritus (i.e., *Malenka*, ostra-

TABLE 4. COMPARISON OF DIET COMPOSITION AMONG THREE SIZE CLASSES OF LARVAL *Dicamptodon tenebrosus* COLLECTED BETWEEN 21 JULY AND 20 SEPT. 1989. Values listed as proportion of total prey (%N) and proportion of stomachs containing prey (%F).

Prey taxon	Salamander size (SVL)					
	25–45 mm		46–70 mm		>70 mm	
	%N	%F	%N	%F	%N	%F
<i>Paraleptophlebia</i>	37.2	69.4	35.0	81.5	25.7	82.2
<i>Baetis</i>	13.4	37.6	17.2	55.6	17.7	48.9
Heptageniidae	9.2	43.5	15.7	62.0	19.7	51.1
<i>Ameletus</i>	0.4	2.4	0.7	17.6	4.4	20.0
<i>Calineuria</i>	1.4	8.2	1.8	13.0	2.4	13.3
<i>Malenka</i>	2.6	11.8	1.4	8.3	0.8	4.4
<i>Polycentropus</i>	9.4	2.0	4.9	26.9	6.8	31.1
Limnephilidae	0.6	2.4	0.3	2.8	1.2	6.7
<i>Lepidostoma</i>	0.8	4.7	1.3	8.3	3.6	8.9
<i>Eubrianax</i>	0.8	3.5	4.3	25.9	3.6	13.3
Chironomidae	13.0	43.5	4.8	29.6	3.2	15.5
Ostracoda	10.6	27.1	2.3	12.0	1.2	6.7
Miscellaneous	8.0	78.0	10.3	68.4	9.7	67.3
No. of salamanders	84		110		54	

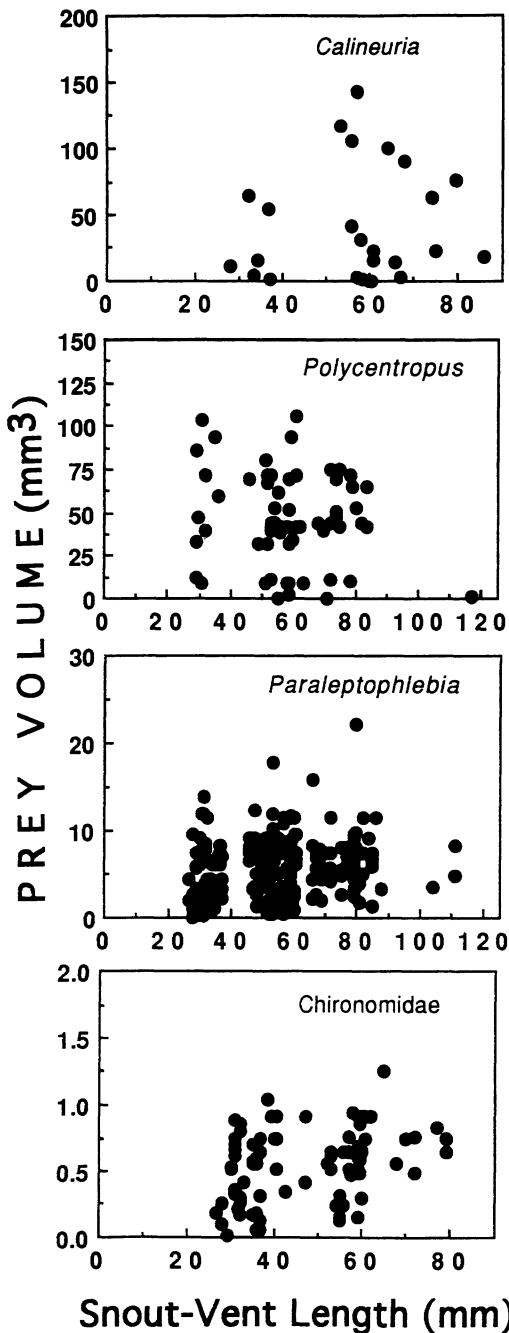


Fig. 5. Relationships between salamander size and volumes of the most abundant prey taxa within the four most frequent insect orders found in their stomach contents. *Calineuria californica*  $R^2 = 0.014$ ,  $P = 0.876$ ,  $n = 26$ ; *Polycentropus* sp.  $R^2 = 0.023$ ,  $P = 0.213$ ,  $n = 61$ ; Chironomidae  $R^2 = 0.132$ ,  $P = 0.004$ ,  $n = 76$ ; *Paraleptophlebia* sp.  $R^2 = 0.021$ ,  $P = 0.048$ ,  $n = 234$ .

cods, and Chironomidae), or are cryptic on stone surfaces (i.e., *Eubrianax*). Such characteristics should combine to reduce encounters between individuals of these prey types and larval salamanders. Another group of prey consistently underrepresented in the diet were case-building caddisfly larvae (Limnephilidae and *Lepidostoma*). Johansson (1991) demonstrated that certain types of cases reduce predation by fish on caddisfly larvae, which may in part explain the negative electivities observed here.

Often predators that exhibit strong diel activity patterns have characteristic peaks in feeding intensity that correspond to peaks in activity (e.g., Hoar, 1942; Kesler and Munns, 1991). Larval *D. tenebrosus* do not follow this pattern. Instead, they appear to feed continuously, both during the day when they are inactive under cover and at night when they are more active and exposed on the streambed surface. Petranka and Petranka (1980) showed a similar pattern for pond-dwelling *Ambystoma opacum*. They hypothesized that the shift in activity and habitat use corresponded to shifts in activity of zooplankton prey. Some benthic invertebrates have been shown to increase their activity and use of substrate surfaces at night (e.g., Elliott, 1968; Kovalak, 1978; but see Allan et al., 1986, for contrasting result). Thus, the increase in activity without a concomitant increase in feeding intensity observed here for larval *D. tenebrosus* might be partially explained as a response to differences in prey availability resulting from shifts in prey activity and microhabitat use. Increased activity at night might also be influenced by reduced prey visibility that could effectively reduce encounter rates. In simple feeding trials, I found that reactive distances were significantly greater and encounter rates significantly higher for heptageniid mayfly and *Calineuria* nymphs during the day than at night (unpubl. data). A perceived reduction in prey density may cause a switch in search behavior from a strictly sit-and-wait to a more active search mode (Anthony et al., 1992). Increased nocturnal activity may also be a response to reduced risk of predation by fish or other visual predators (e.g., Holomuzki, 1986; Stangel and Semlitsch, 1987).

A number of studies have demonstrated ontogenetic shifts in the diet and foraging behavior of larval salamanders (e.g., Dodson and Dodson, 1971; Petranka, 1984; Leff and Bachmann, 1986). Gape-limitation is most often the mechanism controlling the size of prey consumed by different predator size classes (Zaret, 1980). Consequently, as salamanders grow, they tend to include larger prey in their diet (Collins and

Holomuzki, 1984; Petranka, 1984). Larval *D. tenebrosus* tended to follow this pattern as illustrated by the positive relationship between salamander size and volumes of the largest and smallest dietary items. These relationships were not very strong, however, suggesting that salamander size may not be the best predictor of prey size in the diet. Comparisons of predator-prey size relationships for individual taxa also indicated that small larvae were not gape-limited for many of the most abundant prey types, and they were potentially able to consume large proportions of the available size ranges of these taxa. For example, although there were significant positive relationships between prey size and salamander size for two of the smaller common prey, *Paraleptophlebia* and chironomidae, these were apparently not the result of smaller salamanders being restricted to consuming smaller size classes of these taxa because even the smallest salamanders consumed *Polycentropus* and *Calineuria* individuals several times larger than the largest *Paraleptophlebia* and nearly 100 times larger than the largest chironomid eaten. Consequently, large and small larvae consume similar size ranges of common prey, whereas only large larvae are capable of consuming rare, large prey (i.e., small salamanders, juvenile fish, and large invertebrates such as megalopterans and odonates). The observation that all salamander size classes include large proportions of small prey in their diet is likely influenced by the structure of benthic macroinvertebrate assemblages in streams, which tend to be dominated numerically by small taxa and early instars of larger taxa (Morin and Nadon, 1991). So, even though per capita encounter rates may be lower for small prey, and they are generally underrepresented in salamander diets, their generally high densities result in their being consumed fairly frequently.

Ontogenetic diet shifts are often strongly influenced by spatial or temporal shifts in habitat use (Werner and Gilliam, 1984). Dodson and Dodson (1971) and Leff and Bachmann (1986, 1988) found that pond-dwelling tiger salamander larvae (*Ambystoma tigrinum*) shift from feeding on zooplankton in the open water column when they are very small to include a larger proportion of benthic prey when they are large. This shift in habitat use and diet is influenced both by limb development, allowing larvae to switch from swimming to crawling, and by an increase in gape, allowing them to consume larger prey. Such shifts may also be driven by changes in susceptibility to predators (Holomuzki, 1986; McWilliams and Bachmann, 1989b). In general, small streams do not have

stable open water habitats or well-developed planktonic communities. Consequently, stream-dwelling salamander larvae are obligate benthic feeders with limited opportunities to shift among drastically different habitats. Thus, the potential for ontogenetic habitat shifts, and associated diet shifts, should be stronger in pond-dwelling than in stream-dwelling salamander larvae. Larval *D. tenebrosus* do not appear to shift habitats as they grow. All sizes of larvae were found under similar size cover objects and within the same range of depths and current velocities throughout the stream. Activity patterns were also similar among different size larvae.

In general, diet composition was very similar among coexisting size classes of larval *D. tenebrosus*, although relative abundances of certain prey types varied somewhat. Moreover, the considerable dietary overlap observed indicates that food resources were not strongly partitioned among coexisting larval size classes, as has been shown for many pond-dwelling salamanders (Anderson, 1968; Hassinger et al., 1970; Dodson and Dodson, 1971). Petranka (1984) found little difference in habitat use or activity patterns and also found high dietary overlap among larval *Eurycea bislineata* size classes in an intermittent Kentucky stream. He concluded that small size differences between coexisting larval size classes reduced the extent to which gape-limitation influenced ontogenetic diet shifts. This explanation probably does not apply to larval *D. tenebrosus* since size differences among coexisting size classes are considerably greater than for most aquatic salamander larvae, including *E. bislineata*.

Despite inclusion of a large proportion of small prey in their diet, larval *D. tenebrosus* appear to be size selective. In a companion paper (Parker, 1993), I showed that the mechanisms responsible for overrepresentation of large prey in the larval salamander diet include increases in reactive distance and encounter rates as prey size increases and a greater likelihood that large prey will be attacked once encountered. In addition, larger prey provide greater energetic return in terms of biomass consumed per handling time suggesting that larval salamanders may optimize their rate of energy intake by selectively consuming larger prey (e.g., Krebs, 1978). This preferential predation on large, active taxa, and on the largest individuals within certain taxa, could have an important influence on the structure of the benthic macroinvertebrate community. Size-selective predation is a common feature of predator-prey interactions in a variety of aquatic environments (e.g., Wer-

ner and Hall, 1974; Gilson and Benson, 1979; Newman and Waters, 1984). Moreover, size-selective predation by vertebrate predators has been shown to be the mechanism determining the abundance and size distribution of certain prey populations and, thus, the organization of invertebrate communities (Brooks and Dodson, 1965; Dodson, 1970; Sprules, 1972). If, through selective predation, larval *D. tenebrosus* have disproportionately strong negative effects on larger members of their prey communities, they could act as a keystone species (Paine, 1966) in small headwater streams in which they are the dominant vertebrate predator.

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## Interpopulational Variation in Fecundity and Egg Size in Southern Brook Lamprey, *Ichthyomyzon gagei*

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**Environmental influences on absolute fecundity and egg size of southern brook lamprey were investigated for 19 geographically diverse populations in the southeastern United States. Within each population, absolute fecundity increased with total length. No evidence of atresia was found during the postlarval period. Significant differences in absolute fecundity, adjusted to a common size, were observed among populations. Absolute fecundity increased linearly with growth rate for a specific population sex ratio and ambient pH. At low pH, fecundity increased linearly with the proportion of males in a population. At approximately neutral pH, fecundity decreased linearly with the proportion of males. Maximum egg diameter, adjusted to correspond to that at maturity, varied among populations but was not consistently correlated with maternal size. Egg diameter varied for females from the various creeks but was not related to absolute fecundity, population sex ratio, or any of the abiotic characteristics measured.**

**L**IFE-HISTORY traits in fish populations are thought to reflect the collective epigenetic responses of individuals to environmental quality (Balon, 1990). Interpopulation differences in life-history traits variously have been related to ambient biotic and abiotic conditions for several teleosts (Bagenal, 1966; Messieh, 1976; Marsh, 1980). A popular view is that these responses are directed toward maintaining or even enhancing fitness (Mann and Mills, 1979; Heins and Baker, 1987). Intropopulational epigenetic responses are largely unstudied in lampreys despite their primitive phylogeny and the wide range of environments some species inhabit. The

transition by sea lamprey, *Petromyzon marinus*, from anadromy to a life cycle completed entirely in freshwater was accompanied by a shortened juvenile period (Beamish, 1980; Halliday, 1991), smaller size at maturity (Applegate, 1950; Beamish and Potter, 1975), lower fecundity (Vladykov, 1951; Hardisty, 1964), and oscillating sex ratios (Heinrich et al., 1980; Houston and Kelso, 1991). Sex ratios of least brook, *Lampetra aepyptera* (M. F. Docker and F. W. H. Beamish, pers. comm.) and southern brook lamprey, *Ichthyomyzon gagei* (Beamish, 1993) varied dramatically among populations in response to water quality and larval density and growth rates.